Seed dispersal by deer

Student report
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Endozoochorous seed dispersal by roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*) and fallow deer (*Dama dama*) in a semi-natural landscape

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Picture front page: female roe deer in Friesland (the Netherlands). It Frykse Gea.

Abstract

This report discusses a study on endozoochorous seed dispersal by roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*) and fallow deer (*Dama dama*) in a semi-natural landscape. In three areas on the Veluwe samples are taken of three different parts of the digestive tract to determine seed survival rate and potential dispersal by deer. In two areas droppings are collected to determine number of viable seeds and species in dung.

In total 10 plant species are present in droppings and rectum samples and can be dispersed. Deer species dispersed mainly common plant species. No significant differences are found between digestive stages and between deer species for number of viable seeds and plant species. Seed survival rate (rectum/rumen ratio) was the highest in roe and red deer (>600%) and the lowest in fallow deer (>200%). Species survival rate was highest in roe deer (100%) and lowest in fallow deer (28.6%). Fallow deer droppings contained significantly more seeds than red and roe deer droppings and significantly more plant species than roe deer droppings. Based on the results of this research roe deer seem most selective of the three deer species, because absolute number of seeds and plant species is lowest. Fallow deer seem least selective. Seed and plant species survival is the highest in roe deer, which suggests that roe deer are most inefficient digesters.

Based on this study endozoochorous seed dispersal by deer seems of little importance for dispersal of plant species in a semi-natural landscape, because only a small range of common species (n=10) is germinating in rectum samples and droppings.

Samenvatting

In dit verslag worden de resultaten van een onderzoek naar interne zaadverspreiding door reeën (*Capreolus capreolus*), edelherten (*Cervus elaphus*) en damherten (*Dama dama*) in een semi-natuurlijk landschap besproken. In drie gebieden op de Veluwe zijn monsters genomen uit drie verschillende delen van het verteringsstelsel om zaadoverleving en potentiële zaadverspreiding te bepalen. In twee van de drie gebieden zijn uitwerpselen verzameld om het aantal levenskrachtige zaden en soorten in mest te bepalen.

In totaal zijn 10 verschillende plantensoorten gevonden in uitwerpselen en monsters uit het rectum (endeldarm). Reeën, edelherten en damherten verspreidden vooral algemene plantensoorten. Het aantal levenskrachtige zaden en plantensoorten in monsters uit het verteringsstelsel verschilde niet significant tussen de verteringsstadia en tussen reeën, edelherten en damherten. Zaadoverleving (rectum/rumen ratio) was het hoogst in reeën en edelherten (>600%) en het laagst in damherten (>200%). Overleving van soorten was het hoogst in reeën (100%) en het laagst in damherten (28,6%). Uitwerpselen van damherten bevatten significant meer zaden dan uitwerpselen van reeën en edelherten en significant meer plantensoorten dan reeën. Gebaseerd op de resultaten van dit onderzoek lijken reeën het meest selectief, omdat het absolute aantal zaden en plantensoorten in monsters het laagst is. Damherten lijken het minst selectief. Reeën lijken te beschikken over de minst efficiënte vertering, omdat overleving van zaden en plantensoorten het hoogst is.

Gebaseerd op de resultaten van deze studie lijkt interne zaadverspreiding door reeën, edelherten en damherten niet van groot belang voor de verspreiding van plantensoorten, omdat slechts een klein scala algemene soorten (n=10) kiemt in monsters uit het rectum en uitwerpselen.

Introduction

Seed dispersal is essential for the viability of plant populations and for colonisation of new habitats (Poschlod *et al.*, 1996). It results in genetic variation and allows plant populations to adapt to changing environmental conditions and to survive diseases (Willson, 1992). The fragmentation of the current landscape results in long distances and barriers between populations, which causes a reduction of normal migration of organisms.

In Europe species-rich grasslands and heathlands are decreasing as a result of agricultural intensification, bush encroachment and fragmentation of the landscape (Bakker & Berendse, 1999). The potential for restoration of these areas depend on a-biotic (e.g. atmospheric deposition of nutrients and the water level) and biotic constraints (e.g. an impoverished seed bank and a limited seed dispersal range). Most seeds present in the seed bank include long-term persistent, non-target species (Hutchings & Booth, 1996), while seeds of target species are under-represented and transient or short-term persistent. When seeds required for restoration of a target area are not present in the seed bank nor established in the vegetation they have to be dispersed from elsewhere. Dispersal factors are wind, water, man, machines and animals (Bakker *et al.*, 1996). Wind is an overestimated dispersal factor, because most seeds travelling by wind do not cover long distances, especially concerning viable and thus heavier seeds (Zijlstra, 1992; Strykstra *et al.*, 1998). Dispersal by animals (zoochory) might be an opportunity for seeds to be transported over longer distances. Seeds can be attached to fur or hoofs (epizoochory), they can be transported through the digestive system (endozoochory) or they can be carried (synzooochory). Research on epi- and endozoochory showed that a large amount of plant species have the possibility to attach to the fur or to survive digestion (e.g. Welch, 1985; Malo *et al.*, 1995; Malo & Suárez, 1995; Fisher, 1996; Pakeman, 1998; Pakeman *et al.*, 2002; Heinken *et al.*, 2002). Most studies focus on dispersal by domesticated animals as cattle and sheep (e.g. Gardener *et al.*, 1993 a, b; Fisher, 1996; Kiviniema, 1996; Pakeman, 1998; Pakeman *et al.*, 2002; Vos, 2001), while dispersal data on wild animals are largely lacking (Heinken *et al.*, 2002). These wild animals might be a good factor for long distance dispersal because they do not mind human borders and exchange between different areas. In this study endozoochorous seed dispersal by deer is investigated. Dispersal distance depends on retention time and range of action of particular animal species (Bonn & Poschlod, 1998). Based on home range and gut passage time, deer might have the possibility to contribute to long-distance dispersal (table 1). Potential range of internal seed dispersal depends on seed supply, feeding strategies of the animal, survival of seeds through the digestive tract and attractiveness of the parent plant. Anatomy of the digestive system (Hofmann, 1989) and body size (Kleiber, 1947) determine feeding strategies. Small species require more energy per unit body weight and need relatively high quality diets to satisfy their requirements (Demment &Van Soest, 1985; Gordon & Illius, 1994).

Table 1. The home range (ha) and the mean gut passage time (hours) of roe deer and red deer

Species	Home range (ha)	Territory length (T_1, m)	Reference	Mean gut passage time (hrs)	Reference
Roe deer	2-24	140-190	Tufto et al, 1996	19-36	Holand, 1994
Red deer	40-1598	632-4000	Szemethy et al, 1994	27-41	Milne *et al.*, 1978

The aim of this study is to determine the potential internal seed dispersal by roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*) and fallow deer (*Dama dama*) in a semi-natural landscape.

Sub questions are:
1. Are deer capable of internal seed dispersal?
2. What is the quantity of seeds and the composition of plant species dispersed?
3. What is the seed survival rate through the digestive tract of deer?
4. Are there differences between roe deer, red deer and fallow deer?

The hypothesis is that deer are capable of internal seed dispersal (Malo & Suárez, 1995; Heinken *et al.*, 2002).
Plant species composition in deer dung will be determined by food intake. Roe deer are concentrate selectors (Hofmann, 1989) which feed on high quality diets, dominated by dicotyls (Tixier & Duncan, 1996). Red and fallow deer are intermediate feeders (Hofmann, 1989) which are known to feed mainly on grasses (van de Veen, 1979; Prins, 1995). All deer species are expected to disperse *Calluna vulgaris* in late autumn and winter, because diets are dominated by heath when quality of other food plants is decreasing (van de Veen, 1979; Prins, 1995).
Most seeds and species are expected to be present in rumen, because exposure to digestive processes was short. If seeds are as good digestible as foliage, seed survival rate will be comparable to digestion efficiency of food. In equal sample sizes seed content in rectum will be 100% compared to rumen if seeds are as good digestible as foliage. When more than 100% of the seeds is present in rectum samples seeds are considered to survive digestion well. Characteristics of seeds determine survival chances. Low weighted seeds are expected to be abundant in rectum samples and droppings because they are better survivors of herbivore digestion (Pakeman *et al.*, 2002).
Roe deer, red deer and fallow deer are expected to disperse different plant species based on their differences in diet. Absolute number of seeds and plant species is expected to be lowest in roe deer, because they are concentrate selectors (Hofmann, 1989) and can define food intake very precisely. Fallow deer are expected to disperse the highest absolute number of seeds and plant species, because of all three deer species in this study they are most comparable to grass and roughage feeders (Hofmann, 1989), which are least selective in food intake. Seed and plant species survival is expected to be the highest in roe deer, because their digestion is short and relatively inefficient and therefore seeds are least damaged.

In samples of the digestive tract and in droppings of deer viable seeds and plant species were identified to determine the quantity of seeds and plant species composition that could be dispersed by deer. Potential dispersal is determined because it is not known if species recorded actually germinate in a field situation or if they reach a suitable site for establishment. Samples of alimentary tract represent different digestive stages to study seed survival through the tract. Plant species and seeds dispersed by the three different deer species will be compared to each other.

Methods

Study areas

The study is carried out in three different sites, all situated on the Veluwe (the Netherlands): "Landgoed Staverden, "Noorderheide" and" "ASK Oldenbroek" (map 1).

Landgoed Staverden

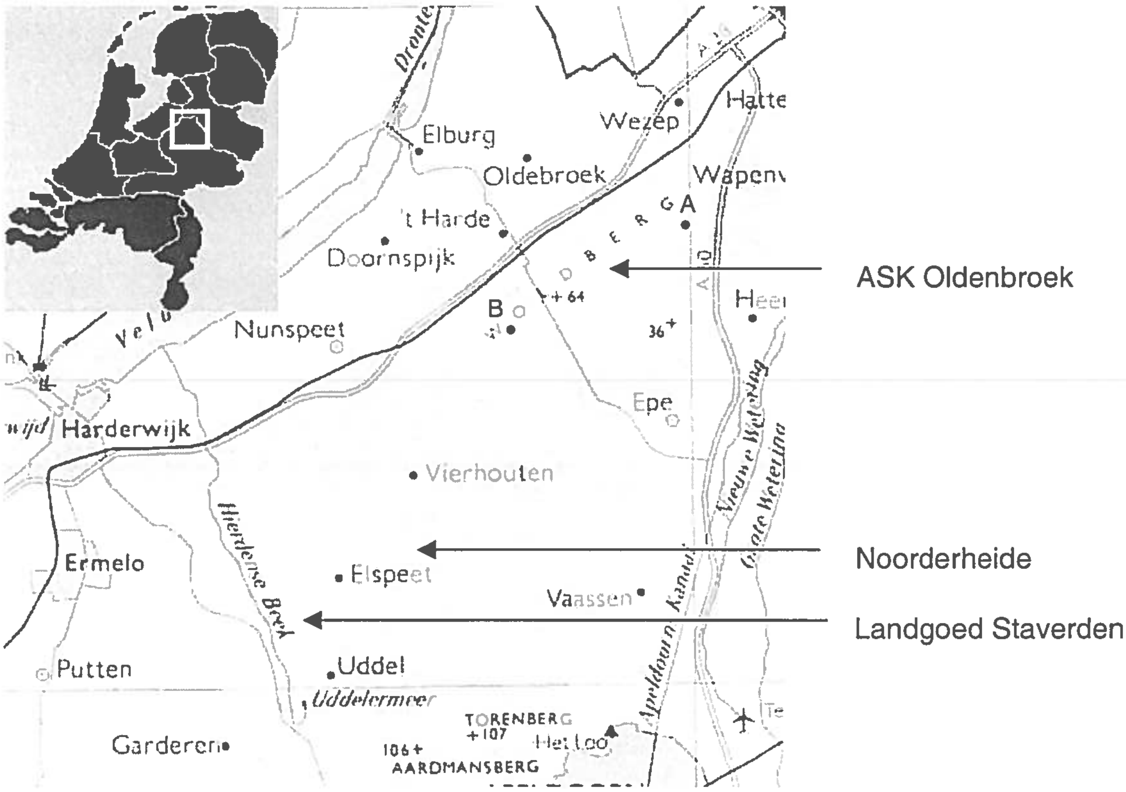
Landgoed Staverden (734 ha) is situated in the Northwest of the Veluwe, near Garderen (about 10 kilometres Southeast of Harderwijk). Landgoed Staverden is a nature reserve possessed by "Het Gelders Landschap". The area is mainly a mixture of deciduous and pine forest (365 ha) combined with grasses, ferns, and brambles. Large parts of the area are leased agricultural lands (300 ha) with *Lolium perenne* grasslands. Some heathland (35 ha), dominated by *Calluna vulgaris*, is present. The remaining area consists of semi-natural grasslands (Ras-Willems & Ras, 1978; Verwoerd, pers. comm., 2003). Deer species present are roe deer and red deer. The total number of red deer varies between 20 and 80, because they exchange with surrounding areas. About 70 roe deer are present (Verwoerd, pers. comm., 2003).

Noorderheide

Noorderheide is situated in the Northwest of the Veluwe, near Vierhouten (about 8 kilometres South of Nunspeet). Noorderheide is a nature reserve possessed by "Staatsbosbeheer". The area consists of heathlands, mainly dominated by *Calluna vulgaris*, sometimes in combination with *Agrostis capillaris*, *Erica tetralix* or *Vaccinium vitis-idaea* (Altenburg & Wymega, 1997). Next to the Noorderheide is the "Vierhouterbos" situated, which is woodland. Deer species present are roe deer, red deer and fallow deer.

ASK Oldenbroek

ASK Oldenbroek is situated in the north of the Veluwe, near 't Harde (about 20 kilometres Southwest of Zwolle). The area is a military terrain with extensive heathland, subdivided in two parts. The eastern part is mainly dominated by extensive *Calluna vulgaris* heathlands where hardly any *Deschampsia flexuosa* is present. The western part contains less extensive *Calluna vulgaris* heathlands. This site is partly dominated by *Deschampsia flexuosa* and *Molinia caerulea*. The total area is surrounded by woodland. There are different types of woodland with oak (*Quercus robur*) and Scots pine (*Pinus sylvestris*) combined with other species as *Deschampsia flexuosa* and *Vaccinium myrtillus* (Haveman *et al.*, 2002; pers. obs., 2002). Deer species present are roe deer and red deer.



Map 1. An overview of the study sites on the Veluwe. Point A and B in ASK Oldenbroek mark the sites where droppings are collected. (De Kleine Bosatlas, Wolters-Noordhoff)

Seeds in digestive tract

Samples of digestive tracts (DT samples) of shot deer are collected in three areas from October through November (table 2). DT samples of red deer are collected in ASK Oldenbroek and Landgoed Staverden, DT samples of fallow deer are collected in the Noorderheide and DT samples of roe deer are collected in the Landgoed Staverden. Hunters sampled three parts of the digestive tract: rumen, abomasum and rectum (Photo 1). Different parts represent different digestive stages: rumen represents an early, abomasum an intermediate and rectum a late digestive stage. DT samples were washed in sieves to remove gastric juices. Stratification was done at 5 degrees Celsius for two weeks, counting from the date the animal was shot. After stratification DT samples were homogenised in a sieve and spread out on trays with sterile sand and soil. Seedlings were identified and counted during 3.5 months. After identification seedlings were removed. Plants not positively identified, but growing so large to prevent other seeds to germinate where grown separately until identification was possible. Sieving and germination of DT samples in the greenhouse was done according to the seed bank method (Ter Heerdt *et al.*, 1996), also used by Vos (2001). To determine the potential presence of viable seeds in the soil and in the greenhouse, control trays with sterile sand and soil, but without DT samples were placed in the greenhouse.
Fresh weight of DT samples was measured. Subsamples were dried at 70°C for 2 days and weighted to determine dry/fresh weight ratio.

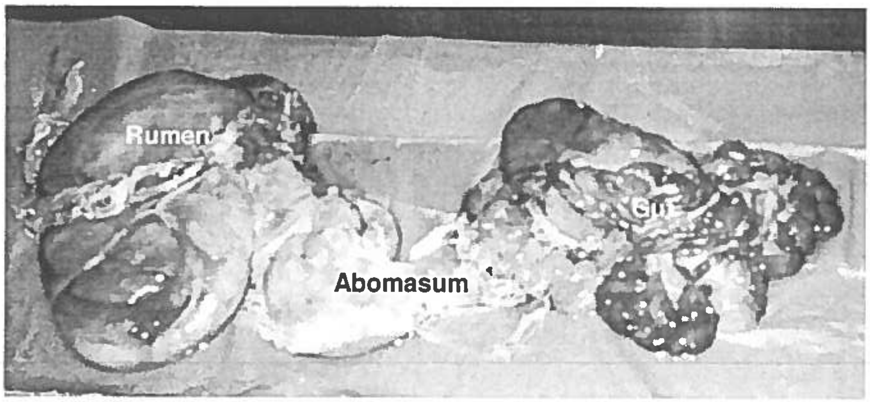


Photo 1. Digestive tract of a roe deer. Rectum is not visible in this picture, it forms the end of the gut. (Photo by Ciska Veen)

Table 2. Total number of DT samples of the digestive tract of shot deer per area. Between brackets the number of samples used in this report.

	Staverden	't Harde	Vierhouten
Roe deer	2 (2)	-	-
Red deer	3 (3)	5 (5)	-
Fallow deer	-	-	8 (5)

Seeds in droppings

In two of the study sites droppings of deer are collected (table 3). In Noorderheide droppings of roe, red and fallow deer are collected in the last week of November 2002. In ASK Oldenbroek droppings of red deer, which spent time on the heathland (pers. comm. Timmer, 2002), are collected at two different sites at 3 December 2002. Site A was situated in the eastern part of the terrain and site B in the western part (map 1).

Fresh weight of droppings was measured. After two weeks of stratification (5°C) droppings were treated as DT samples. Seedlings were identified during two months.

Table 3. Number of droppings collected per area.

	ASK Oldenbroek	Noorderheide
Roe deer	-	10
Red deer	12 (site A 7/ site B 5)	10
Fallow deer	-	10

Data analysis

Number of seeds germinated in DT samples was transformed to number of seeds germinated per 100 gram dry weight based on dry/fresh weight ratio of subsamples. Data on seed germination in droppings were transformed to number of seeds per 100 gram dry weight using the mean dry weight of rectum samples. No dry weight of droppings was measured, because samples were too small.

Mean number (+/- SE) of seeds and plant species is calculated per digestive stage, per deer species and per area.

Number of seeds and plant species per individual in different digestive stages were compared using non-parametric analysis of variances (Kruskal-Wallis). When digestive stages differed significantly a post-hoc Tukey's test was used to specify differences between groups. Correlation between number of seeds in digestive stages is tested using Spearmans rho for correlation. Differences between deer species and between areas were compared in the same way, as well for samples as for droppings.

All statistic analyses were carried out using SPSS 11.0. Data are tested with non-parametric tests variances are not homogeneous (Levene's test) and data were not normally distributed.

Results

In total 10 different species are present in droppings and rectum samples: *Agrostis capillaris, Cerastium fontanum, Juncus bufonius, Lolium perenne, Luzula campestris, Molinia caerulea, Persicaria maculosa, Plantago major, Rumex acetosella* and *Vaccinium* sp. (table 4, table 6).

Seeds in digestive tract

In total 20 different plant species are observed in samples of the digestive tract (table 4). Total number of species is highest in rumen samples and lowest in rectum samples. Not all species found in abomasum and rectum samples were present in rumen samples. 10 of 20 species present in samples belong to the family of the Poaceae (table 4). 7 of these Poaceae germinated in red deer samples, 4 in fallow deer samples and no Poaceae were found in roe deer samples (appendix 6).
Seeds present in DT samples have a relative low dispersule weight. In the database comparative plant ecology (Hodsgon *et al.*, 1995) seeds are classified in 6 weight categories, all seeds present in DT samples belong to the categories with low weights (table 4).

Table 4. Mean number of viable seeds (+/- SE) per plant species present in rumen, abomasum and rectum samples per 100 gram dry weight. Total number of species is given at the bottom of the graph. In the last columb a categorie for dispersule weight is given: 1 represents seeds with low dispersule weight and 6 represents seeds with high dispersule weight (Hodsgon *et al.*, 1995). Categories: 1 = <0.20 mg, 2 = 0.21-0.50 mg, 3 = 0.51-1.00 mg, 4 = 1.01-2.00 mg, 5=2.01-10.00 mg, 6 = >10 mg.
* n.k. = dispersule weight category is not known.

Species	Family	Rumen	SEM	Abomasum	SEM	Rectum	SEM	Weight
Agrostis canina	Poaceae	2,1	+/- 0,7	-		-		1
Agrostis capillaris	Poaceae	13,9	+/- 3,9	92,6	+/- 24,2	139,5	+/- 26,8	1
Agrostis stolonifera	Poaceae	-		1,7	+/- 0,6	-		1
Cerastium fontanum	Caryophyllaceae	-		0,6	+/- 0,2	-		1
Deschampsia flexuosa	Poaceae	0,2	+/- 0,1	-		-		2
Festuca rubra	Poaceae	1,0	+/- 0,3	1,0	+/- 0,4	-		3
Hieracium sp.	Asteraceae	0,5	+/- 0,2	0,6	+/- 0,2	-		n.k.*
Juncus bufonius	Juncaceae	0,8	+/- 0,3	4,3	+/- 1,1	9,9	+/- 1,9	1
Juncus effusus	Juncaceae	0,6	+/- 0,1	174,5	+/- 47,7	-		1
Molinia caerulea	Poaceae	-		-		1,3	+/- 0,5	3
Persicaria maculosa	Polygonacea	0,2	+/- 0,1	-		0,9	+/- 0,3	n.k.*
Phleum pratense	Poaceae	-		1,7	+/- 0,6	-		2
Poa annua	Poaceae	0,7	+/- 0,2	-		-		2
Poa pratensis	Poaceae	1,0	+/- 0,3	-		-		2
Poa trivialis	Poaceae	1,0	+/- 0,3	1,7	+/- 0,6	-		1
Rumex acetosella	Polygonacea	0,5	+/- 0,2	-		18,3	+/- 6,5	2
Sagina procumbens	Caryophyllaceae	-		3,0	+/- 0,9	-		1
Stellaria media	Caryophyllaceae	0,6	+/- 0,2	-		-		2
Urtica dioica	Cannabaceae	0,3	+/- 0,1	-		-		1
Vaccinium sp.	Ericaceae	22,8	+/- 5,3	5,8	+/- 1,1	-		2
Total number of plant species		15		11		5		

There is no significant correlation between number of seeds per DT sample per 100 gram dry weight in rumen and abomasum ($p = 0.103$), in abomasum and rectum ($p = 0.162$) and in rumen and rectum ($p = 0.226$). Though, increase in number of seeds in early digestive stages leads to increase in number of seeds in late digestive stages (appendix 2).

No significant differences are found between digestive stage for number of seeds (p = 0.720) or number of plant species (p = 0.178). Though in abomasum most viable seeds are present and least viable seeds are present in rumen (figure 1). Number of plant species is lowest in rectum samples (figure 1).

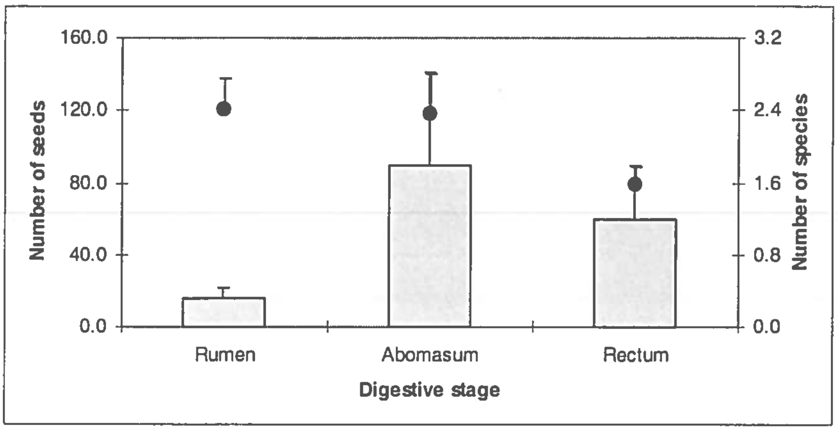
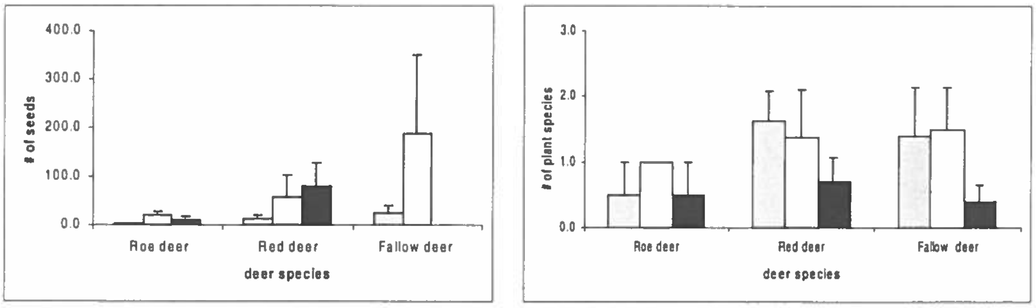


Figure 1. Mean number of viable seeds and species present per 100 gram dry weight. Bars represent mean number of seeds present and dots represent mean number of species present. Error bars represent SE of mean. (Rumen n=15, abomasum n=14, rectum n=14).

No significant difference is found between deer species (figure 2) for neither mean number of seeds nor mean number of plant species. No significant difference is found between areas (appendix 1) for mean number of seeds or mean number of plant species (P-values: appendix 4). Digestive stages did not differ significantly for mean number of seeds (p = 0.694) or mean number of plant species (p = 0.215). Though mean number of plant species is lowest in rectum samples, except for roe deer in which mean number of plant species in rectum is equal to mean number in rumen (figure 2b).



(a) (b)

Figure 2. Mean number of viable seeds (a) and mean number of plant species (b) per deer species per 100 gram dry weight (roe deer, n = 2; red deer, n = 8; fallow deer, n = 5). Different coloured bars represent different digestive stages: rumen ( ), abomasum (□) and rectum (■). Error bars represent SE of mean.

In equal volumes of rumen and rectum samples, rectum samples of roe and red deer contained over 600% of the number of seeds in rumen and fallow deer over 200% (figure 3). For roe deer 100% of the number of plant species in rumen was present in roe deer. This percentage was lower for red deer (44,0%) and for fallow deer (28,6%) (figure 3).

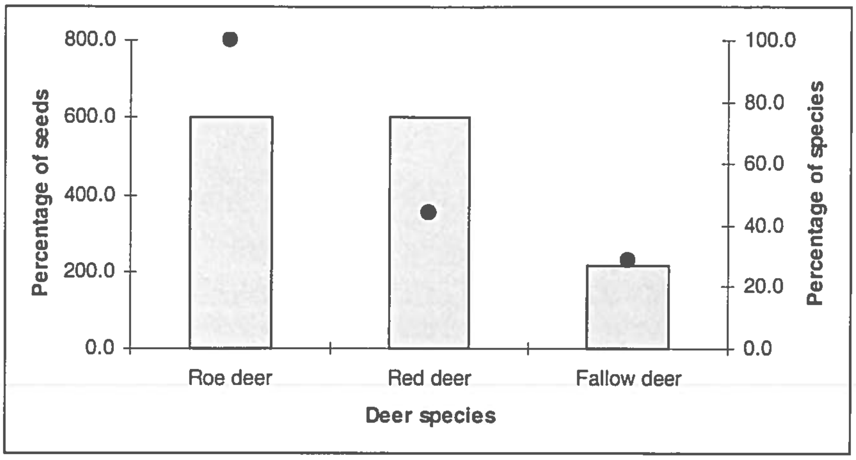


Figure 3. Percentage of viable seeds and species in rumen present in rectum samples per 100 gram dry weight. Bars represent percentage of seeds and dots represent percentage of species.

Seeds in droppings

Except for roe deer, all droppings contained viable seeds. Significant difference is found between number of seeds ($p = 0.002$) and number of species ($p = 0.003$) (table 5). Fallow deer droppings contained a significant higher number of seeds than roe deer and red deer and a significant higher number of species than roe deer (figure 4).

	# seeds	# species
roe deer	a	a
red deer	a	ab
fallow deer	b	b

Table 5. Different letters indicate significant differences between deer species considering mean number of seeds or mean number of species.

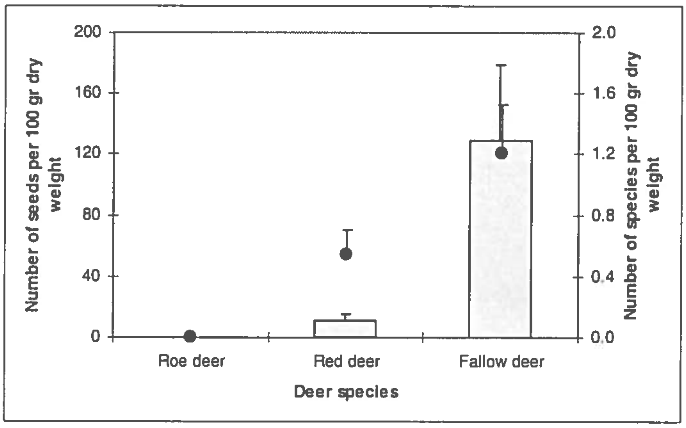


Figure 4. Mean number of viable seeds (bars) and mean number of species (dots) germinated in droppings per 100 gram dry weight. Error bars represent SE of mean. Roe deer (n=10), red deer (n=22) and fallow deer (n-10).

Table 6. Mean number (+/- SE) of viable seeds in droppings. (N) represents droppings of Noorderheide and (ASK) represents droppings of ASK Oldenbroek. On the bottom of the table total number plant species and mean number of plant species are given.

		Roe deer (N)		Red deer (N)		Fallow deer (N)		Red deer (ASK)	
Species	**Family**	MEAN	*SEM*	MEAN	*SEM*	MEAN	*SEM*	MEAN	*SEM*
Agrostis cappilaris	Poaceae	-		12,2	+/- 5,4	0,3	+/- 0,3	3,1	+/- 1,9
Cerastium fontanum	Caryophyllaceae	-		-		1,3	+/- 0,9	-	+/- 0,0
Lolium perenne	Poaceae	-		-		0,7	+/- 0,7	-	+/- 0,0
Luzula campestris	Juncaceae	-		-		-		0,3	+/- 0,3
Plantago major	Plantaginaceae	-		-		1,2	+/- 1,2	0,6	0,6
Vaccinium sp.	Ericaceae	-		-		125,0	+/- 49,7	5,4	+/- 5,4
Total number of species		-		1,0		5,0		4,0	

Discussion

Quantity of seeds and species

As expected seeds are capable of surviving digestion of deer and of germination in dung. Mean number of viable seeds and species in rectum samples were comparable to mean number of seeds and species in roe deer droppings in a temperate forest in Northern Germany (Heinken *et al.*, 2002). Mean number of seeds in droppings was lower than in DT samples, which might be due to time of the year (end of November) they are collected. It will be better to collect droppings throughout the vegetational period from May till October, also done by Heinken *et al.* (2002), then it is possible to determine total potential seed dispersal. Total number of species recorded in rectum samples (n=5) and droppings (n=6) in this study is low in comparison to number of species in droppings of red deer (n=66) and fallow deer (n=67) in a Mediterranean area (Malo & Suárez, 1995).

In a Mediterranean area cattle dispersed more different species than red deer and fallow deer (Malo & Suárez, 1995). Total number of species recorded in this study was also lower than total number of species recorded in cattle dung (18 and 21 different species for two sites) in areas with oligotrophic and mesotrophic plant communities in the north of the Netherlands (Vos, 2001). Roe, red and fallow deer and cattle are on a feeding selectivity gradient (Hofmann, 1989), where roe deer are most selective (concentrate selectors) and cattle are least selective (Grass and roughage feeders). This might explain the higher number of species present in dung of cattle.

Composition of plant species

Roe deer select for low fibre contents and were expected to disperse least grasses (van de Veen, 1979; Hofmann, 1989; Prins, 1995; Duncan *et al.*, 1998). Grass species (family of Poaceae) were recorded in DT samples and droppings of red and fallow deer, but no grass species were present in neither DT samples (appendix 5) nor droppings (table 6) of roe deer. In cattle dung in the north of the Netherlands grass species were present (7 of 18 and 7 of 21 at two different sites), and belonged to the most dispersed species: *Poa* sp. (*P. trivialis, P. annua, P. pratensis*) (Vos, 2001). *Poa* sp. were hardly present in deer droppings and samples, what might be due to low seed supply in autumn. *Agrostis capillaris* was abundant in rectum samples (table 4) and droppings of deer (table 6), though this plant species was barely present in cattle dung pats what might be due to unripe seeds at the time of dung collection (Vos, 2001). *Juncus* sp. were present in both cattle and deer dung.

Calluna vulagris was expected to be eaten and to survive digestion (small, round seeds), but no heath was present in neither droppings nor rectum samples. Maybe grass was still available in sufficient amounts or heath is not yet germinated after three months in the greenhouse. *Vaccinium* sp. was abundant in droppings of fallow deer. *Vaccinium* sp. are fruit bearing plants, where fruits are considered to attract herbivores for endozoochorous seed dispersal, hence it is expected that these species are adapted to passage of the digestive tract (Heinken *et al.*, 2002).

Seed survival rate

Number of seeds present in equal sample sizes of rumen and rectum were compared (figure 3). Percentage of seeds present in rectum samples was much more than 100% for all deer species, which means that seeds are less digested than the rest of the food (foliage) and therefore became concentrated in rectum samples. Seed survival rate per plant species could not be calculated because seed intake by deer was not continuous. Seeds present in rectum samples were taken in a couple of days before seeds present in rumen. When seed intake is continuous plant species composition in rectum samples would be a reflection of the composition in rumen samples, only fewer species will be present because survival differs. In abomasum and rectum samples species were recorded that were not found in rumen samples (table 4). It is possible an individual switched between area or plant species, consequently different seeds are ingested during a couple of days.

Rectum/rumen ratio was highest for roe deer and lowest for fallow deer considering both number of seeds and number of plant species (figure 3), but mean number of seeds and species in DT samples were lowest in roe deer samples (figure 2, appendix 5). In droppings number of seeds and species present in fallow deer samples was significant higher than in roe deer samples. According to the classification of ruminants (Hofmann, 1989) roe deer were considered to have most inefficient digestion, what causes increased survival chances for seeds and plant species and thus a high rectum/rumen ratio. Roe deer belong to the concentrate selectors who define food intake very precisely, what might explain low numbers of seeds and plant species in samples. Fallow deer are described as intermediate feeders, but very close to grass and roughage eaters (Hofmann, 1989) and therefore they are the opposite from roe deer. Their digestion is most efficient and food intake is least selective of the deer species investigated in this study.

As expected total number of plant species was highest in rumen samples (table 1). Plant species differ in survival chances of digestion due to species characteristics (Janzen, 1984; Pakeman *et al.*, 2002), some species are not capable of surviving digestion and do not germinate in rectum samples. Seed characteristics as low seed weight and high long-evity index increase seed survival rate (Pakeman *et al.*, 2002). All seeds present in DT samples in this study were classified in low seed weight categories (Hodsgon *et al.*, 1995). Janzen (1984) described in his "foliage is the fruit" hypothesis that large herbivores might be an important dispersal factor for small seeded herbaceous plants. Herbivores consume seeds while eating the foliage of the plant.

Method

Number of viable seeds and species present in samples and droppings show large variation, which can be due to several factors. Samples are collected in three areas with different plant species composition and seed supply, therefore seed intake by animals varies between areas. Within the sampling period (September till November) seed supply can vary because of seasonal effects. Samples should be collected in a period of several weeks instead of several months to rule out seasonal effects. Seed density and species richness in dung samples varies significantly depending on collection date (Malo & Suárez, 1995). Plants are identified for three months, which is short in comparison to Vos (2001) and Pakeman *et al.* (2002) who identified plants for 5 and 6 months, respectively. It is possible seeds will germinate after three months, though it is unlikely because in trays where seedlings were identified and removed in November, hardly any seedlings were found in December and January. When samples are air-dried (Malo & Suárez, 1995; Pakeman *et al.*, 2002; Heinken *et al.*, 2002) growth of fungi during stratification might be reduced, so stratification time can be increased to six weeks (Heinken *et al.*, 2002), which stimulates seeds to germinate in the greenhouse.

Variation can also be due to differences between individual animals, for example in digestion and food intake. These differences can be ruled out when sample size is increased. Individual variation can be increased by selection by hunters. Deer are shot as a population regulation measure and hunters try to select for weak animals to keep the population healthy. These animals might behave different from healthy animals in food selection, food intake and digestion.

Number of deer shot within an area is not sufficient to rule out individual differences. It will be better to collect droppings of all deer species within one area. Sample size can be enlarged and droppings can be collected during a longer period.

Conclusions

The aim of this study was to determine the potential quantity of seeds and composition of plant species endozoochorously dispersed by deer. Results showed deer are capable of seed dispersal, because plants were present in rectum samples and droppings. Though, endozoochorous seed dispersal will be of little importance for plant species. Only a small number of common plant species germinates in droppings and rectum samples of the three deer species investigated. Plant species most present in droppings and rectum samples were *Agrostis capillaris, Juncus bufonius, Rumex acetosella* and *Vaccinium* sp.
Between samples of deer species no significant difference is found for number of viable seeds and species. Droppings of fallow deer contained significant more seeds than droppings of roe and red deer and significant more species than roe deer. Roe deer seem to be most selective of all deer species, because absolute number of seeds and species in droppings and digestive tract samples present is lowest. Roe deer samples and droppings contained no grass species, which are known for high fibre contents. Rectum/rumen ratio was highest in roe deer, therefore they seem to have most inefficient digestion. Lowest rectum/rumen ratio was found in fallow deer, they seem to have a more efficient digestion.s
Total rectum/rumen ratio for seeds was higher than 100% in all deer species, so seeds seem to be good survivors of digestion. No survival rate can be determined for individual plant species, because little data are present.

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Appendices

Appendix 1: Mean number of seeds and species present per area

Mean number of viable seeds (figure 5) and mean number of plant species (figure 6) ordered by area.

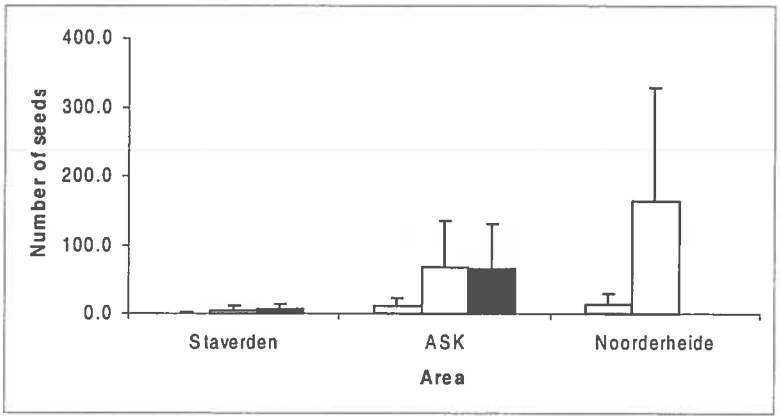


Figure 5. Mean number of viable seeds per area. Error bars represent SE of Mean. Different coloured bars represent different digestive stages rumen ( ), abomasum (□) and rectum (■).

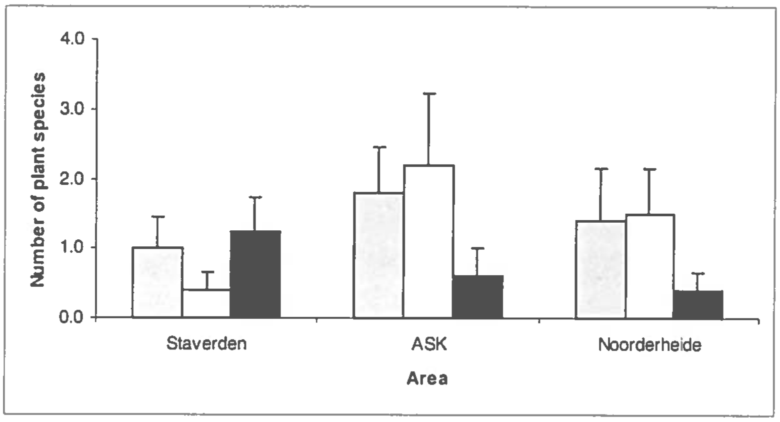


Figure 6. Mean number of plant species per area. Error bars represent SE of Mean. Different coloured bars represent different digestive stages rumen ( ), abomasum (□) and rectum (■).

Appendix 2: Correlation digestive stages

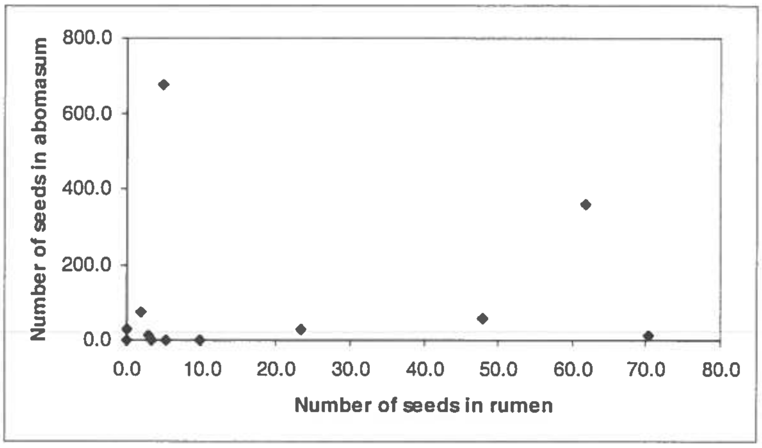


Figure 7. Number of seeds per 100 gram dry weight in rumen plotted against number of seeds per 100 gram dry weight in abomasum. Spearman's rho for correlation is 0.437, p = 0.103.

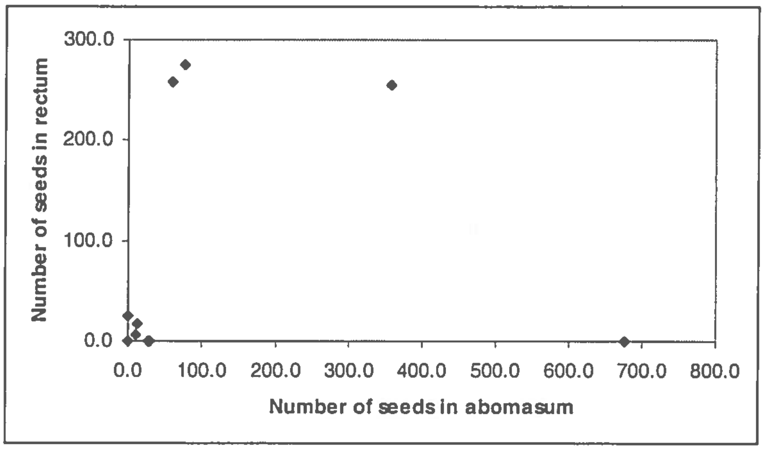


Figure 8. Number of seeds per 100 gram dry weight in abomasum plotted against number of seeds per 100 gram dry weight in rectum. Spearman's rho for correlation is 0.412, p = 0.162.

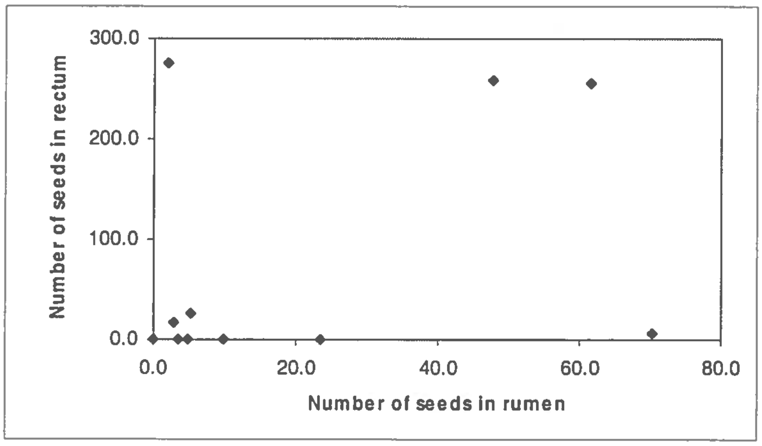
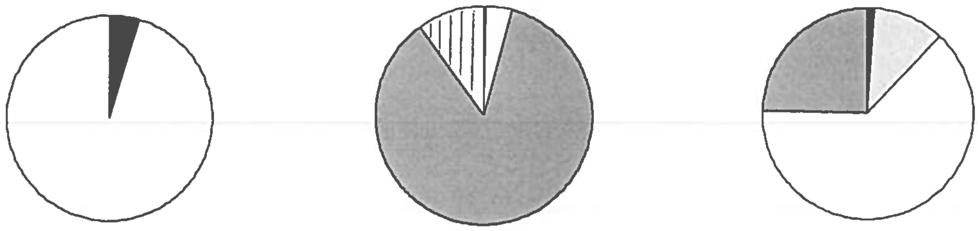


Figure 9. Number of seeds per 100 gram dry weight in rumen plotted against number of seeds per 100 gram dry weight in rectum. Spearman'ss rho for correlation is 0.360, p = 0.226.

Appendix 3. Relative contribution plant families

Relative contribution of different plant families in samples of roe, red and fallow deer (figure 10). Roe deer samples contain mainly Juncaceae (figure 10a). Poaceae dominate plant family composition in red deer (figure 10b). Fallow deer samples contain mainly Juncaceae, but also Poaceae are present a lot (figure 10c).



(a) **(b)** **(c)**

Figure 10 a, b, c. Plant family composition in samples of (a) roe deer, (b) red deer and (c) fallow deer. Different colours represent different plant families: Caryophalleceae (■), Ericaceae ( ), Juncaceae (□), Poaceae (■), Other families (▥).

Appendix 4. Comparison between deer species

Table 7. P-values representing differences between the three deer species per digestive stage

	Number of seeds	Number of species
Rumen	0.581	0.500
Abomasum	0.589	0.788
Rectum	0.938	0.895

Table 8. P-values representing differences between the three areas per digestive stage

	Number of seeds	Number of species
Rumen	0.520	0.685
Abomasum	0.376	0.304
Rectum	0.945	0.864

Appendix 5: Mean number of seeds per deer species and per area

Table 9. Mean number (+/- SE) of viable seeds in rumen, abomasum and rectum ordered by deer species. At the bottom of the table number of plant species is given.

		Total number of seeds **						**Number of seeds in rectum**					
		Roe deer	*SEM*	Red deer	*SEM*	Fallow deer	*SEM*	Roe deer	*SEM*	Red deer	*SEM*	Fallow deer	*SEM*
Agrostis canina	Poaceae	-		1,3	*+/- 0,8*	-		-		-		-	
Agrostis capillaris	Poaceae	-		114,1	*+/- 32,5*	61,4	*+/- 30,8*	-		87,8	*+/- 41,2*	51,7	*+/- 51,7*
Agrostis stolonifera	Poaceae	-		1,1	*+/- 0,6*	-		-		-		-	
Arabidopsis thaliana	Brassicaceae	-		-		-		-		-		-	
Cerastium fontanum	Caryophyllaceae	-		0,3	*+/- 0,2*	-		-		-		-	
Chenopodium album	Chenopdiaceae	-		-		-		-		-		-	
Deschampsia flexuosa	Poaceae	-		-		0,2	*+/- 0,1*	-		-		-	
Festuca rubra	Poaceae	-		1,3	*+/- 0,5*	-		-		-		-	
Galium uligonosum	Rubiaceae	-		-		-		-		-		-	
Hieracium sp.	Asteraceae	-		0,7	*+/- 0,3*	-		-		-		-	
Juncus bufonius	Juncaceae	15,4	*+/- 5,7*	4,3	*+/- 1,7*	-		8,8	*+/- 8,8*	11,0	*+/- 3,1*	-	
Juncus effusus	Juncaceae	13,5	*+/- 7,8*	1,3	*+/- 0,6*	134,2	*+/- 80,0*	-		-		-	
Molinia caerulea	Poaceae	-		-		1,3	*+/- 0,8*	-		-		1,3	*+/- 1,3*
Persicaria maculosa	Polygonacea	-		0,6	*+/- 0,3*	-		-		1,8	*+/- 0,5*	-	
Phleum pratense	Poaceae	-		1,1	*+/- 0,6*	-		-		-		-	
Poa annua	Poaceae	-		0,2	*+/- 0,1*	0,3	*+/- 0,2*	-		-		-	
Poa pratensis	Poaceae	-		0,6	*+/- 0,4*	-		-		-		-	
Poa trivialis	Poaceae	-		1,7	*+/- 0,7*	-		-		-		-	
Rumex acetosella	Polygonacea	-		11,8	*+/- 6,7*	-		-		18,3	*+/- 13,1*	-	
Sagina procumbens	Caryophyllaceae	-		-		2,4	*+/- 1,4*	-		-		-	
Stellaria media	Caryophyllaceae	1,5	*+/- 0,8*	-		-		-		-		-	
Urtica dioica	Cannabaceae	-		0,2	*+/- 0,1*	-		-		-		-	
Vaccinium sp.	Ericaceae	-		-		27,4	*+/- 9,4*	-		-		-	
Number of plant species		3		15		7		1		4		2	

** total number of seeds is the sum of seeds in rumen, abomasum and rectum

Table 10. Mean number (+/- SE) of viable seeds in rumen, abomasum and rectum ordered by area. At the bottom of the table number of plant species present is given.

		Total number of seeds **						Number of seeds in rectum					
		Staverden	*SEM*	ASK	*SEM*	Noorderheide	*SEM*	Staverden	*SEM*	ASK	*SEM*	Noorderheide	*SEM*
Agrostis canina	Poaceae	-		2,1	*+/- 1,2*	-		-		-		-	
Agrostis capillaris	Poaceae	-		182,5	*+/- 48,8*	61,4	*+/- 30,8*	-		87,8	*+/- 54,9*	51,7	*+/- 51,7*
Agrostis stolonifera	Poaceae	-		1,7	*+/- 1,0*			-		-		-	
Arabidopsis thaliana	Brassicaceae	-		-		-		-		-		-	
Cerastium fontanum	Caryophyllaceae	-		0,6	*+/- 0,3*	-		-		-		-	
Chenopodium album	Chenopdiaceae	-		-		-		-		-		-	
Deschampsia flexuosa	Poaceae	-		-		0,2	*+/- 0,1*	-		-		-	
Festuca rubra	Poaceae	-		2,0	*+/- 0,8*	-		-		-		-	
Galium uligonosum	Rubiaceae	-		-		-		-		-		-	
Hieracium sp.	Asteraceae	-		1,1	*+/- 0,4*	-		-		-		-	
Juncus bufonius	Juncaceae	11,4	*+/- 3,4*	1,7	*+/- 1,0*	-		9,9	*+/- 5,8*	-		-	
Juncus effusus	Juncaceae	5,8	*+/- 3,2*	1,7	*+/- 1,0*	134,2	*+/- 80,0*	-		-		-	
Molinia caerulea	Poaceae	-		-		1,3	*+/- 0,8*	-		-		1,3	*+/- 1,3*
Persicaria maculosa	Polygonacea	0,9	*+/- 0,4*	-		-		0,9	*+/- 0,9*	-		-	
Phleum pratense	Poaceae	-		1,7	*+/- 1,0*	-		-		-		-	
Poa annua	Poaceae	-		0,4	*+/- 0,2*	0,3	*+/- 0,2*	-		-		-	
Poa pratensis	Poaceae	-		1,0	*+/- 0,6*	-		-		-		-	
Poa trivialis	Poaceae	-		2,7	*+/- 1,1*	-		-		-		-	
Rumex acetosella	Polygonacea	-		18,8	*+/- 10,6*	-		-		18,3	*+/- 18,3*	-	
Sagina procumbens	Caryophyllaceae	-		-		2,4	*+/- 1,4*	-		-		-	
Stellaria media	Caryophyllaceae	0,6	*+/- 0,3*	-		-		-		-		-	
Urtica dioica	Cannabaceae	0,3	*0,2*	-		-		-		-		-	
Vaccinium sp.	Ericaceae	-		-		27,4	*+/- 9,4*	-		-		-	
Number of plant species		5		13		7		2		2		2	

** total number of seeds is the sum of seeds in rumen, abomasum and rectum

Appendix 6: Number of seeds per individual in digestive tract

Table 11. Number of seeds present per plant species per individual in Landgoed Staverden per 100 gram dry weight. RG- (roe deer) and EH- (red deer) numbers represent individuals. Ree 1S represents a roe deer sample from Staverden without a number. Sample EH-6914 contains only rumen and abomasum, because no rectum samples was taken. At the bottom of the table total number of seeds and species per individual is given.

		EH 6913			EH 6914		EH 6915			Ree 1S			RG 14		
Species	**Family**	Rumen	Abomasum	Rectum	Rumen	Abomasum	Rumen	Abomasum	Rectum	Rumen	Abomasum	Rectum	Rumen	Abomasum	Rectum
Juncus buffonius	Juncaceae	4.16	-	21.95	-	-	-	-	-	-	13.28	17.54	-	-	-
Juncus effusus	Juncaceae	-	-	-	-	-	1.70	-	-	-	-	-	-	27.05	-
Persicaria maculosa	Polygonacea	1.04	-	3.66	-	-	-	-	-	-	-	-	-	-	-
Stellaria media	Caryophyllaceae	-	-	-	-	-	-	-	-	2.91	-	-	-	-	-
Urtica dioica	Cannabaceae	-	-	-	-	-	1.70	-	-	-	-	-	-	-	-
Total number of seeds		5.20	-	25.61	-	-	3.41	-	-	2.91	13.28	17.54	-	27.05	-
Total number of plant species		2	-	2	-	-	2	-	-	1	1	1	-	1	-

Table 12. Number of seeds present per plant species per individual in ASK Oldenbroek per 100 gram dry weight. EH- (red deer) numbers represent individuals. At the bottom of the table total number of seeds and species per individual is given.

		EH 7061			EH 7067			EH 7068			EH 7071			EH 7072		
Species	**Family**	Rumen	Abomasum	Rectum	Rumen	Abomasum	Rectum	Rumen	Abomasum	Rectum	Rumen	Abomasum	Rectum	Rumen	Abomasum	Rectum
Agrostis canina	Poaceae	-	-	-	10,4	-	-	-	-	-	-	-	-	-	-	-
Agrostis capillaris	Poaceae	-	-	-	5,2	24,6	-	59,0	342,8	255,5	-	-	-	-	42,3	183,3
Agrostis stolonifera	Poaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	8,5	-
Cerastium fontanum	Caryophyllaceae	-	-	-	-	-	-	-	2,8	-	-	-	-	-	-	-
Festuca rubra	Poaceae	-	-	-	5,2	4,9	-	-	-	-	-	-	-	-	-	-
Hieracium sp.	Asteraceae	-	-	-	-	-	-	2,7	2,8	-	-	-	-	-	-	-
Juncus bufonius	Juncaceae	-	-	-	-	-	-	-	8,4	-	-	-	-	-	-	-
Juncus effusus	Juncaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	8,5	-
Phleum pratense	Poaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	8,5	-
Poa annua	Poaceae	-	-	-	-	-	-	-	-	-	-	-	-	1,9	-	-
Poa pratensis	Poaceae	-	-	-	-	-	-	-	-	-	5,0	-	-	-	-	-
Poa trivialis	Poaceae	-	-	-	-	-	-	-	-	-	5,0	-	-	-	8,5	-
Rumex acetosella	Polygonacea	-	-	-	2,6	-	-	-	-	-	-	-	-	-	-	91,6
Total number of seeds		-	-	-	23,4	29,5	-	61,7	356,8	255,5	9,9	-	-	1,9	76,2	274,9
Total number of species		-	-	-	4	2	-	2	4	1	2	-	-	1	5	2

Table 15. Number of seeds per plant species in droppings of fallow deer in Noorderheide per 100 gram dry weight. The first row shows the number of the individual. V represents the area Noorderheide (Vierhouten) and DA represents the deer species fallow deer.

Species	Family	V-DA-1	V-DA-2	V-DA-3	V-DA-4	V-DA-5	V-DA-6	V-DA-7	V-DA-8	V-DA-9	V-DA-10
Agrostis capillaris	Poaceae	-	-	-	-	-	-	-	-	3,1	-
Cerastium fontanum	Caryophyllaceae	-	-	-	-	6,6	-	-	-	-	6,8
Lolium perenne	Poaceae	-	-	-	-	-	-	-	-	-	6,8
Luzula campestris	Juncaceae	-	-	-	-	-	-	-	-	-	-
Plantago major	Plantaginaceae	-	-	-	-	-	-	-	-	-	-
Vaccinium sp.	Ericaceae	-	11,2	246,2	424,2	99,7	5,6	-	-	333,2	129,8
# seeds		-	11,2	258,0	424,2	106,4	5,6	-	-	336,3	143,5
# species		-	1	2	1	2	1	-	-	2	3

Table 16. Number of seeds per plant species in droppings of fallow deer in ASK Oldenbroek per 100 gram dry weight. The first row shows the number of the individual. H represents the area ASK Oldenboek ('t Harde) and EH represents the deer species red deer. A and B represent collection sites A and B (map 1).

Species	Family	H-EH-A1	H-EH-A2	H-EH-A3	H-EH-A4	H-EH-A5	H-EH-A6	H-EH-A7	H-EH-B1	H-EH-B2	H-EH-B2	H-EH-B4	H-EH-B5
Agrostis capillaris	Poaceae	-	-	-	-	-	-	-	8,5	-	-	7,3	21,5
Cerastium fontanum	Caryophyllaceae	-	-	-	-	-	-	-	-	-	-	-	-
Lolium perenne	Poaceae	-	-	-	-	-	-	-	-	-	-	-	-
Luzula campestris	Juncaceae	-	-	-	-	-	-	-	-	3,5	-	-	-
Plantago major	Plantaginaceae	-	-	-	-	-	-	-	-	-	-	-	7,2
Vaccinium sp.	Ericaceae	-	-	-	-	-	-	-	-	-	-	-	64,5
# seeds		-	-	-	-	-	-	-	8,5	3,5	-	7,3	93,1
# species		-	-	-	-	-	-	-	1	1	-	1	3